

Bogumiła DOMICZ-STYCZYŃSKA

A tentative morphological characteristic of the parasitic fly

Próba morfologicznej charakterystyki muchówki pasożytnej

The aim of the investigation was to characterize the parasitic *Diptera* by establishing the features which adapt it to the parasitic way of life. A group of parasitic *Diptera* which could give as full a picture as possible of parasitological adaptations, viz., the family *Hippoboscidae*, was the object of the investigation. Its representatives, ectoparasites of mammals and birds, are closely related either to one host species, or to several kindred ones or to a wide range of them. This is connected with the degree of morphological specialization of a parasite.

Hippoboscidae used to be assigned to the so called *Pupipara*, a group considered by older writers, e.g., Speiser, 1902 particularly compact and clearly distinct from other *Diptera*, while later writers, such as Hennig, 1941 and Bequaert, 1942 were of a different opinion, stressed the far-going differences between *Hippoboscidae*, *Nycterobiidae*, *Strelidae* and *Braulidae* and related each of these families with oviparous *Diptera*. Nevertheless the biological feature of all parasitic *Diptera* which used to be called *Pupipara* consists not so much in pupiparity as in larviparity, a kind of adaptation to the parasitic way of life.

The author dealing with *Pupipara* did not on the whole try to establish general common features of these *Diptera*. Only a very general characteristic may be drawn up on the basis of monographic studies by Massonat (1909), Hennig (1941), and Bequaert (1942). It covers:

(1) larviparity, stressed by all authors although it is well known that this way of development can be observed in free-living forms in the imaginal stage, e.g., in *Oestridae*;

(2) specific morphological changes in the general structure of these *Diptera*, due to their way of living, above all rudimentary or reduced wings.

These features had been treated only descriptively and rather qualitatively than quantitatively in previous studies, with the exception of a paper by Massonat (1909) related in subject matter to the present one. But its general statements are rather modest compared to its extensive descriptions. Moreover Massonat gave simple measurements of length and width and not figures for their mutual relations, which give a better idea of both their shape and its changes.

Material and methods

The species of the family *Hippoboscidae* occurring in Poland, viz., *Lipoptena cervi* L., *Hippobosca equina* L., *Ornithomyia avicularia* L., *Stenopteryx hirundinis* L. and *Crataerhina pallida* Latr. were used as basic material for the investigation. The order in which I mention the species examined roughly coincides with the degree of adaptation to the parasitic way of life and their growing monophagism.

In order to set off its parasitic features a comparison was made with a free-living, also haemophagous *Diptera* species — *Stomoxys calcitrans* L.

The material investigated came mainly from the collections of Sł. Kozłowski and was supplemented with my own specimens. It included a total of 45 specimens, a few of each species. The measurements of tagmata and legs were made by means of a measurement ocular. It was not necessary to scale the microscope as further discussion is based on indices and not on measurements.

The measurements of parts of the body of the insects examined are given in Table I, which contains average figures for various species and indices for various parts of the body. The table is a starting point for further analysis.

General bodily proportions and relation of tagmata

The species examined show more or less shortening of various tagmata of the body. But mere descriptions of the shortening give a completely subjective picture which does not admit of

Table I
Measurements (in the scale of the ocular) and indices of various parts of the body of the *Diptera* examined.

	<i>S. calcitrans</i> L. long. lat. ind.		<i>L. cervi</i> L. long. lat. ind.		<i>H. equina</i> L. long. lat. ind.		<i>O. avicularia</i> L. long. lat. ind.		<i>S. hirundinis</i> L. long. lat. ind.		<i>C. pallida</i> Latr long. lat. ind.							
coxa I femur I tibia I tarsus I	2.1	1.7	1.20	2.2	1.9	1.10	3.8	3.6	1.05	3.0	2.6	1.15	2.8	2.5	1.10	4.2	3.8	1.10
	10.5	1.6	6.56	6.1	3.4	1.79	9.7	4.0	2.42	7.8	3.2	2.43	9.2	4.0	2.30	12.5	4.7	2.06
	10.3	1.0	10.30	7.1	1.4	5.07	9.9	2.0	4.95	7.4	1.3	5.69	7.8	1.4	7.00	11.8	1.6	7.37
	10.9	0.5	21.80	4.2	0.9	4.66	5.3	1.4	3.71	5.0	0.9	5.55	5.6	1.0	5.60	9.0	1.7	5.29
coxa II femur II tibia II tarsus II	2.0	1.6	1.25	1.9	2.1	0.90	3.4	3.2	1.06	2.3	1.8	1.30	2.4	2.5	0.96	4.5	2.6	1.73
	12.4	1.5	8.26	8.4	3.2	2.62	12.1	4.0	3.02	10.4	2.3	4.52	10.3	3.6	2.86	13.4	4.3	3.11
	12.1	1.2	10.80	7.9	1.5	5.76	11.7	2.0	5.85	9.0	1.5	6.00	9.4	1.6	5.87	13.2	1.9	6.94
	11.9	0.7	10.70	4.6	1.0	4.60	6.0	1.7	3.62	5.3	0.9	5.88	6.0	1.3	4.61	8.9	1.7	5.23
coxa III femur III tibia III tarsus III	2.4	2.5	0.98	2.9	3.0	0.96	5.2	5.5	0.94	4.4	1.5	2.90	4.0	3.3	1.21	4.6	4.4	1.04
	12.9	1.6	8.06	9.8	2.8	3.50	16.5	3.3	5.00	11.8	2.6	4.53	13.3	3.0	4.43	14.2	4.0	3.55
	11.7	1.3	9.00	8.6	1.6	5.37	14.9	2.2	6.77	11.0	1.2	9.16	9.9	1.5	6.60	12.3	1.9	6.47
	13.6	0.9	15.10	6.1	0.8	7.62	7.3	1.4	5.21	7.7	1.1	7.00	8.2	1.4	5.85	8.8	1.4	6.35
caput thorax abdomen	8.8	12.8	0.68	6.0	9.0	0.66	7.4	11.5	0.64	6.2	9.4	0.65	6.5	9.0	0.72	10.2	9.2	1.10
	18.6	16.1	1.23	10.6	11.3	0.92	18.4	21.1	0.87	10.6	14.6	0.86	8.6	13.2	0.65	9.0	14.6	0.61
	20.2	17.4	1.16	12.6	11.0	1.14	22.9	23.7	0.92	12.2	14.1	0.86	16.1	20.4	0.78	11.1	15.1	0.73

accurate comparison. Shortening indices contained in Table I may give better orientation, yet the most convenient values may be obtained from the application of relations of those indices, i.e., figures expressing mutual relations of the shortening of various tagmata or their groups.

The relation of the shortening of the abdomen and the thorax to that of the head is shown in Table II, in which figures are given which are products of respective indices. It follows from the table that the thorax and abdomen, although generally more shortened than the head (with the exception of *C. pallida* Latr.), show a varying degree of shortening in various species and a varying relation of this shortening to that of the head. This relation amounts to the highest figure in haemophagous yet free-living *Stomoxys calcitrans* L. and in very volatile and not very specific *Lipoptena cervi* L., while it diminishes in *Diptera* more closely connected with their host, and reaches a distinct minimum in *Crataerhina pallida* Latr.

Table II

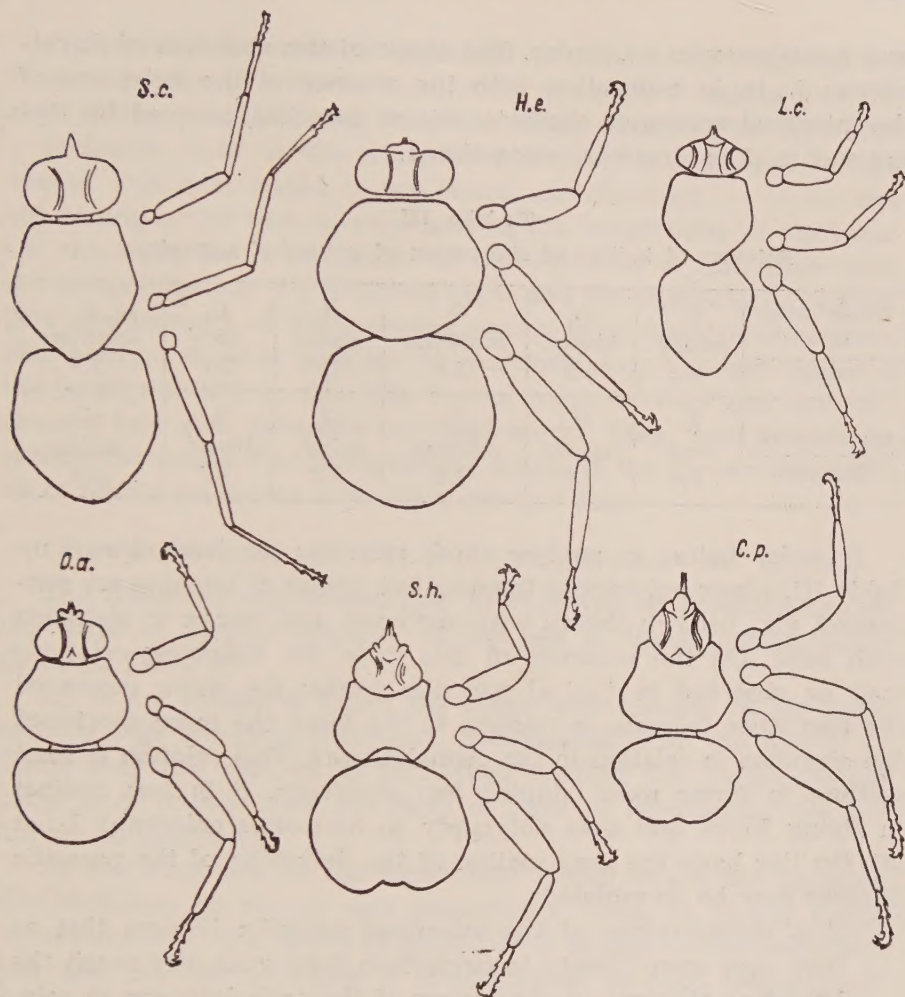
Relation of indices of shortening of thorax and abdomen to those of head.

abdo- men	<i>C.</i> <i>pallida</i>	<i>S.</i> <i>hirundinis</i>	<i>O.</i> <i>avicularia</i>	<i>H.</i> <i>equina</i>	<i>S.</i> <i>calcitrans</i>	<i>L.</i> <i>cervi</i>
caput	0.66	1.08	1.32	1.44	1.70	1.73
thorax	<i>C.</i> <i>pallida</i>	<i>S.</i> <i>hirundinis</i>	<i>O.</i> <i>avicularia</i>	<i>H.</i> <i>equina</i>	<i>L.</i> <i>cervi</i>	<i>S.</i> <i>calcitrans</i>
caput	0.55	0.90	1.32	1.36	1.39	1.89

On the basis of Tables I & II the first section of the definition of the parasitic *Diptera* may therefore be formulated as follows:

With a growing degree of adaptation to parasitism the forms examined show an increasingly distinct higher degree of shortening in abdomen and thorax than head.

The observed proportions of the head are related to the structure and function of the oral apparatus, which in the case of *Crataerhina pallida* Latr. and *Stenopteryx hirundinis* L. is thrust into the skin in a „passive” manner like a wedge pushed by the pressure from the muscles of the thorax, while in *Stomoxys calcitrans* L. the thrusting of the oral apparatus is „active”, i.e., connected with the sawing movement of the labellary apparatus (Švanvič, 1949). The proportions of the abdomen, which is



Diagrams showing bodily proportions of *Diptera* examined

S. c. — *Stomoxys calcitrans* L., *H. e.* — *Hippobosca equina* L., *L. c.* — *Lipoptena cervi* L., *O. e.* — *Ornithomyia avicularia* L., *S. h.* — *Stenopteryx hirundinis* L., *C. p.* — *Crataerhina pallida* Latr.

more shortened in parasites, are related to the situation of the head in a special hollowing so characteristic of *C. pallida* Latr. and *S. hirundinis* L., while the extension of the abdomen is related to the growth of the intestinal parts in those parasites. The proportion of the thorax in *S. calcitrans*, which has well-developed wings is related to the mobility of its head and the extension of motional muscles in each of its three segments, the mesothorax

and metathorax in particular. The shape of the abdomen of *S. calcitrans* L. is, in connection with the absence of the extension of the intestinal apparatus characteristic of parasites, adapted for flying and so it is somewhat streamlined.

Table III
Relation of indices of shortening of groups of tagmata

thorax-abdomen	<i>C. pallida</i>	<i>S. hirund.</i>	<i>O. avicularia</i>	<i>H. equina</i>	<i>L. cervi</i>	<i>S. calcitrans</i>
caput	1.2	1.9	2.6	2.8	3.1	3.5
caput-thorax	<i>L. cervi</i>	<i>H. equina</i>	<i>S. calcitrans</i>	<i>O. avicul.</i>	<i>S. hirund.</i>	<i>C. pallida</i>
abdomen	1.4	1.5	1.6	1.7	1.7	2.3

In order better to analyse these relations we have drawn up Table III, where not various tagmata but groups of tagmata are contrasted, viz., head + thorax with abdomen, and thorax + abdomen with head. On the evidence of this table the following relations may be observed in typical parasitic forms: the more shortened the two other tagmata in relation to the head, the more shortened the abdomen in relation to the cephalothorax. This relation is most distinct in forms most adapted for parasitism, it is less distinct in flying forms and does not apply to *Stomoxys calcitrans* L. at all. On this basis the next section of the definition of the parasitic *Diptera* may be formulated:

It is characteristic of the examined parasitic *Diptera* that as they pass more closely to parasitism they gradually reach the lowest co-efficient of shortening of the cephalothorax in relation to that of the head and the highest co-efficient of shortening of the cephalothorax in relation to that of the abdomen.

As the head is more shortened than the thoracoabdomen and at the same time less shortened than the abdomen itself, it may be assumed that a considerable shortening of the abdomen in a parasite is compensated to some extent by a slight shortening of the thorax. As the cephalothorax is more shortened than the abdomen, and the head of the parasite is least shortened, the general proportions of the body are partly influenced by the lengthening of the head compensated by a certain shortening of the thorax (and a hollowing on its front border).

These relations could be explained as follows: the shape of the head is connected with its function of a wedge thrusting into the skin of the host. But this function which extends the head into a proboscis must at the same time develop the muscles of the thorax and thus result in its lateral development — hence the shortening of the thorax compensating the lengthening of the head. On the other hand the shape of the abdomen is connected with the development of the intestinal parts and the reproductive organs. The development of these organs results in a characteristic recession of the centre of gravity. To counterbalance this and preserve the insect's ability to move the thorax must develop not only sideways but also forwards and backwards. These two tendencies jointly determine the characteristic shape of the thorax the outline of which resembles a hexagon more or less.

Proportions of various segments of legs

The following regularities may be observed on consideration of the shape of various segments of the legs of the examined forms listed in Table I:

(a) in all examined forms the coxae and femores of all three pairs of legs are most shortened, independent from the degree to which they are adapted to parasitism, so that this morphological detail is of no use from the point of view of formulating the definition in question;

(b) the structure of the tibiae and tarsus shows the greatest differentiation in shapes and proportions. Thus, in flying forms (*S. calcitrans* L.) the tarsus of pairs I & II of legs is relatively longest, and the tarsus of pair II is as long as, or even longer than, the tibia. In *L. cervi* L. the tibia and the tarsus is longest in pairs I & II, but the tarsus is longest in pair II. *H. equina* L., *O. avicularia* L., *S. hirundinis* L. and *C. pallida* Latr. have the longest tibia in all three pairs of legs.

Consequently, the function of the coxae and femores would appear to be the same in all examined *Diptera*, while the functions of other segments differ, as free-living forms use them in a different way than parasites do.

Flying forms seem to find a strongly extended tarsus of pairs I & III most useful. The tarsus of pair I also seems to perform the function of a supplementary tactile organ in addition to its adhesive function. *L. cervi* L., although a flying form, distinctly

Table IV
Correlation of leg segments

coxa I	H. equina	S. hirundinis	L. cervi	C. pallida	O. avicularia	S. calcitrans
femur I	L. cervi	C. pallida	S. hirundinis	H. equina	O. avicularia	S. calcitrans
tibia I	H. equina	L. cervi	O. avicularia	S. hirundinis	C. pallida	S. calcitrans
tarsus I	H. equina	L. cervi	C. pallida	O. avicularia	S. hirundinis	S. calcitrans
coxa II	L. cervi	S. hirundinis	H. equina	S. calcitrans	O. avicularia	C. pallida
femur II	L. cervi	S. hirundinis	H. equina	C. pallida	O. avicularia	S. calcitrans
tibia II	L. cervi	H. equina	S. hirundinis	O. avicularia	C. pallida	S. calcitrans
tarsus II	H. equina	L. cervi	S. hirundinis	C. pallida	O. avicularia	S. calcitrans
coxa III	H. equina	L. cervi	S. calcitrans	C. pallida	S. hirundinis	O. avicularia
femur III	L. cervi	C. pallida	S. hirundinis	O. avicularia	H. equina	S. calcitrans
tibia III	L. cervi	C. pallida	S. hirundinis	H. equina	S. calcitrans	O. avicularia
tarsus III	H. equina	S. hirundinis	C. pallida	O. avicularia	L. cervi	S. calcitrans

differs from relations characteristic of free-living forms, as the tibia of pairs I & II of its legs are longest. This is probably connected with their taking over the adhesive function (the recession of the insertions of the muscles of the tarsus). The same applies to the tibiae of all three pairs of legs in typically parasitic forms.

The arrangement of our materials in horizontal rows and vertical columns in Table IV gives a picture of correlations between shapes of various segments of all legs in various species. The horizontal rows in this table are so arranged that species with the lowest index, i.e., with most shortened segments appear on the extreme left, while species with least shortened segments are to be found on the extreme right. Thus, the coxa of pair I is most shortened in *H. equina* L. and most lengthened in *S. calcitrans*, etc.

Table V
Number of correlated features

Species	Number of correlating characteristics
<i>Stomoxys calcitrans</i> L.	9
<i>Lipoptena cervi</i> L.	6
<i>Hippobosca equina</i> L.	6
<i>Ornithomyia avicularia</i> L.	5
<i>Stenopteryx hirundinis</i> L.	5
<i>Crataerhina pallida</i> Latr.	4

Species correlated in the shape of a given segment of a given pair of legs are therefore included in vertical columns. Thus, the coxa of pair I in *S. hirundinis* L. is just as much shortened as the coxa of pair III in *L. cervi* L. and less shortened than the coxa of pair I of this species. It follows from Table V that:

(1) in free-living forms (*S. calcitrans* L.), all segments of pair I, medial segments of pair III and the femur and tarsus of pair III are correlated to each other; this species distinctly differs in this respect from all other, parasitic ones;

(2) no correlation between shapes of various segments can be observed in parasitic species; thus, the coxa of pair I in *S. hirundinis* L. has a different shape than the other segments of the same pair; only the coxa and femur are just as much shortened in pair I of legs; while only the tarsus is just as much shortened as the coxa and femur of pair II and the coxa of pair I.

The following section of the attempted definition of the parasitic *Diptera* may therefore be formulated as follows:

Nearly every segment of legs of the parasitic *Diptera* has a different function and therefore it is shaped in a different way than the other segments of the same pair and the same segment in the other pairs. This implies a gradual disappearance of the correlation of leg segments with increasingly better adaptation to parasitism.

Final conclusions

With a higher degree of adaptation to monophagism the examined parasitic *Diptera* show the less shortened head the more shortened their other tagmata, of which the abdomen is most shortened. The lowest coefficient of shortening of the cephalothorax in relation to the head is accompanied by the highest coefficient of shortening of the cephalothorax in relation to the abdomen (Table II & III).

With a higher degree of adaptation to monophagism the examined parasitic *Diptera* show an even greater discorrelation of leg segments: each of these segments assumes a different shape in each pair, the tibiae being longest in all three pairs of legs or at least in pairs I & III (Table IV & V).

Table VI

Classification of species examined in terms of characteristics searched

With respect to proportions of tagmata (Tab. II, III)	<i>Stomoxys calcitrans</i> L.	<i>Lipoptena cervi</i> L.	<i>Hippobosca equina</i> L.	<i>Ornithomyia avicularia</i> L.	<i>Stenopteryx hirsuticornis</i> L.	<i>Crataerhina pallida</i> Latr.
With respect to discorrelated legs. (Tab. IV, V)	<i>Stomoxys calcitrans</i> L.	<i>Lipoptena cervi</i> L.	<i>Hippobosca equina</i> L.	<i>Ornithomyia avicularia</i> L.	<i>Stenopteryx hirsuticornis</i> L.	<i>Crataerhina pallida</i> Latr.

These data show that investigation into the characteristics of the parasitic *Diptera* which, for methodical reasons, deals separately with the tagmata of the body and leg proportions, its results may finally be presented together, as in Table VI. This table

shows a gradual development of the characteristics discussed as the insect becomes more distinctly parasitic and even more closely connected with the host. If further research on other material confirmed the tendencies we observed, they could be regarded as leading characteristics of the parasitic *Diptera*.

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Author's address:

Państwowy Zakład Higieny, Zakład D.D.D.
Warszawa, Chocimska 24

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STRESZCZENIE

Zadaniem pracy było ustalenie cech, którymi wyróżniają się muchówki z rodziny *Hippoboscidae* i które mogą je charakteryzować jako owady w słabszym lub silniejszym stopniu związane z pasożytniczym trybem życia. Dla ustalenia tych cech autorka wykonała pomiary tagm i odcinków nóg badanych muchówek pasożytnych i ustaliła wskaźniki (tabele I—VI), pozwalające na scharakteryzowanie zmian przystosowawczych w porównaniu z muchówką wolnożyjącą, lecz krwio pijną, jaką jest *Stomoxys calcitrans* L.

Przebadane muchówki pasożytne wraz z rosnącym stopniem przystosowania do monofagizmu, mają głowę tym mniej skróconą, im bardziej skrócone są pozostałe tagmy, z których najsilniej skrócony jest odwłok. Najmniejszemu współczynnikowi skrócenia tułowio-odwłoka w stosunku do głowy towarzyszy największy współczynnik skrócenia głowo-tułowia w stosunku do odwłoka (tabele II, III).

Przebadane muchówki pasożytne wraz z rosnącym stopniem przystosowania do monofagizmu wykazują coraz większy stopień rozkorelowania poszczególnych członów nóg: każdy z tych członów staje się inaczej ukształtowany w każdej parze, przy czym najbardziej wydłużone są tibiae albo wszystkich trzech par, albo przynajmniej I i III pary nóg (tabele IV, V).

Z danych tych wynika, że rozważania nad charakterystycznymi cechami pasożytnych *Diptera*, choć ze względów metodycznych rozpatrujące oddzielnie tagmizację ciała i proporcje nóg, ostatecznie dają się zestawić zgodnie ze sobą, jak na to wskazuje tabela VI. Wykazuje ona stopniowy wzrost omawianych cech w miarę przechodzenia do wyraźniej pasożytniczego trybu życia i coraz silniejszego związania z żywicielem. Zaobserwowane tendencje, gdyby dalsze badania na innym materiale je potwierdziły, uznać by można za przewodnie cechy, charakteryzujące muchówki pasożytne.